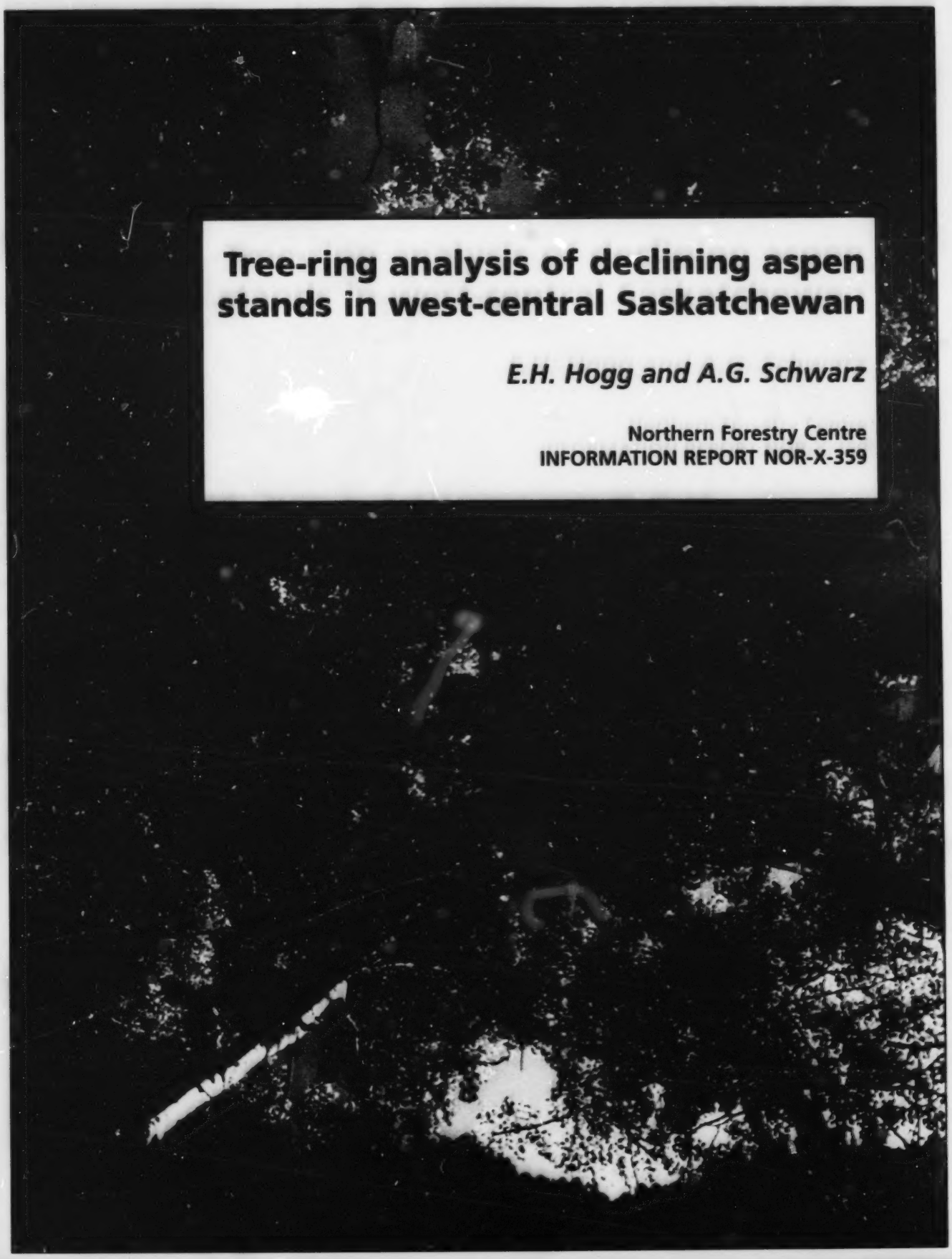

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E.H. Hogg and A.G. Schwarz

Northern Forestry Centre
INFORMATION REPORT NOR-X-359

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TREE-RING ANALYSIS OF DECLINING ASPEN STANDS IN WEST-CENTRAL SASKATCHEWAN

E.H. Hogg and A.G. Schwarz[1]

INFORMATION REPORT NOR-X-359

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ABSTRACT

Recent decline of trembling aspen (*Populus tremuloides* Michx.) near St. Walburg, Saskatchewan, prompted a study to document the onset and progress of aspen decline and to examine how past climate variation and insect defoliation might have contributed to the decline. Tree-ring analysis was conducted on a total of 138 aspen in pure and mixed 50–75-year-old stands, including stands showing heavy decline (more than 40% crown dieback). Past survey records and the presence of light-colored (white) growth rings indicated that stands in the study area were severely defoliated by forest tent caterpillar (*Malacosoma disstria* Hbn.) in 1962–1964 and several years during the period 1979–1990. Regression modeling showed that insect defoliation was the most important factor causing reduced growth in stem basal area, but drought also had a significant influence. During periods with defoliation, stem growth was often reduced to less than 10% of that recorded during the most favorable periods. In the early 1990s, stem growth had recovered in all stands except those in the heavy decline class; however, a late winter thaw followed by severe frost in April 1992 caused a temporary reduction in stem growth and might have contributed to the observed dieback. Long-term productivity of aspen stands in this region will likely depend strongly on the future dynamics of forest tent caterpillar and the incidence of extreme climatic events. Crown dieback is expected to occur when drought occurs in combination with several consecutive years of defoliation.

RÉSUMÉ

Le déclin du peuplier faux-tremble (*Populus tremuloides* Michx.) qui s'est amorcé il y a quelques années dans la région de St. Walburg (Saskatchewan) a incité les auteurs à étudier le début et l'évolution du déclin et le rôle des variations climatiques et des défoliations passées causées par les insectes dans l'apparition du phénomène. Un total de 138 peupliers faux-trembles provenant de tremblaies pures et mélangées de 50 à 75 ans, dont certaines affichaient un taux de dépérissement important (dépérissement de la cime supérieur à 40 %), ont été soumis à des analyses dendrochronologiques. Les résultats de relevés passés et la présence de cernes annuels pâles (blancs) ont révélé que les tremblaies comprises dans la zone d'étude avaient été gravement défoliées par la livrée des forêts (*Malacosoma disstria* Hbn.) en 1962-1964 et, par la suite, pendant de nombreuses années entre 1979 et 1990. À l'aide de modèles de régression, les auteurs ont montré que la défoliation par les insectes était le principal facteur responsable de la réduction de la croissance de la portion basale de la tige; la sécheresse a également joué un rôle significatif à ce chapitre. Durant les périodes de défoliation, la croissance de la tige a souvent chuté à moins du dixième du rythme observé en présence de conditions plus favorables. Au début des années 90, la croissance de la tige était revenue à la normale dans toutes les tremblaies, à l'exception de celles présentant les plus fort taux de dépérissement. Toutefois, un dégel hivernal tardif suivi d'une

vague de froid intense en avril 1992 a ralenti temporairement la croissance de la tige et pourrait avoir contribué au déclin. La productivité à long terme des tremblaies dans la région semble étroitement liée à la dynamique des populations de la livrée des forêts et à la fréquence des événements climatiques extrêmes. D'autres épisodes de dépérissement de la cime devraient se produire chaque fois que des vagues de sécheresse surviendront durant plusieurs années consécutives de défoliation.

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INTRODUCTION

Trembling aspen (*Populus tremuloides* Michx.) is the most important deciduous tree species in the western Canadian boreal forest and commonly grows in pure stands, or stands mixed with white spruce (*Picea glauca* Moench [Voss]) and other boreal conifers (Peterson and Peterson 1992); however, the commercial potential of trembling aspen has only been fully recognized since the early 1980s. As a result, relatively little is known on the ecological and climatic factors controlling the productivity of this species.

Recent decline of trembling aspen in the Bronson Forest, located north of St. Walburg, Saskatchewan, has prompted a collaborative study by Mistik Management Ltd., the Canadian Forest Service (CFS), and the University of Alberta. The overall objectives were to identify the causes and extent of the aspen decline and its ecological and economic impact, and to develop strategies to address reduced harvestable volumes and rejuvenate decadent aspen stands. The present component of this study focuses on understanding how past climate and insect defoliation might have contributed to the observed decline and dieback of aspen in this region. Various definitions for the terms decline and dieback have been proposed (Manion and Lachance 1992). In the present study, decline was used as a general term referring to chronic reductions in forest productivity and health, while dieback (increased branch mortality in tree crowns) was considered to be one of the visible symptoms of decline.

Moisture stress (drought) was considered to be a potential cause of aspen decline because weather conditions during the 1980s were warmer and drier than normal over much of the region. Furthermore, the Bronson Forest is located near the boundary between the boreal forest and the aspen parkland to the south, where aspen productivity is often reduced due to dry climatic conditions (Hogg 1994; Hogg and Hurdle 1995). Thus aspen productivity in the Bronson Forest would be sensitive to weather-related variation in moisture regimes.

Another major stress on aspen in the region is defoliation by insects, particularly forest tent caterpillar (*Malacosoma disstria* Hbn.). Infestations of this insect were recorded for several consecutive years in the late 1980s over a large area of eastern Alberta and western Saskatchewan that included the Bronson Forest (Brandt 1995). Previous studies have established that repeated defoliation by forest tent caterpillar leads to reduced growth (Hildahl and Reeks 1960) and increased stem mortality (Churchill et al. 1964; Hildahl and Campbell 1975) of aspen stands.

No apparent detailed studies have been conducted to determine how trembling aspen responds to the combined effects of insect defoliation and climatic variation. Although dendrochronology can be a powerful means of examining past growth responses of forests, it has seldom been applied to aspen. This is partly because aspen is a short-lived species that is, therefore, of limited usefulness in reconstructing past climates, and also because of the perceived difficulty in reliably identifying and cross-dating annual growth rings.

In a related study at Batoche (research site located northeast of Saskatoon, Saskatchewan), tree rings in aspen were found to be visible under magnification, if cores or disks were carefully prepared and polished. It was noted that abnormally light-colored (white) growth rings were formed during years when outbreaks of forest tent caterpillar were known to have occurred (Hogg 1999).

In the present study, tree-ring analysis was used to determine interannual growth in stem basal area within stands in the Bronson Forest that exhibited various degrees of decline in 1995. The objectives were 1) to conduct analyses of past climatic variation in the Bronson Forest, including the application of a climatic moisture index (Hogg 1997); 2) to reconstruct defoliation histories for individual stands, based on regional insect survey records and the annual frequency of white rings; 3) to compare past patterns of stem growth and white rings in mixed wood and pure stands in various stages of decline; and 4) to use regression modeling as a means of identifying the relative contribution of climate and defoliation as factors governing the growth and decline of these stands.

METHODS

Study Area

All sampling sites were located in the Bronson Forest, within 1 km of Highway 26 between St. Walburg and Loon Lake, Saskatchewan (53°45′ to 53°51′N, and 109°08′W). Forests are predominantly pure aspen with some areas of aspen–white spruce mixed wood. Aspen stands are generally even-aged, with a relatively sparse understory dominated by rose (*Rosa* sp.), fireweed (*Epilobium latifolium* L.), grasses, and occasional regenerating aspen. The terrain is a gently undulating to rolling glacial till plain with medium to moderately textured, orthic gray wooded soils (Rostad and Ellis 1972).

In late summer 1995, a total of six sites were selected and marked. The stand designations for these sites are given in Table 1. Three of the sites (1, 2, and 3) were located in pure stands of trembling aspen that each had adjacent clones in the following classes based on average percentage crown dieback: heavy decline; (>40% dieback); light decline (15–40% dieback) and healthy (<15% dieback). One circular plot with a radius of 10 m was established in each of the decline classes at each of these three sites (total of 9 plots). The remaining three sites (4, 5, and 6) were located in mixed wood stands of non-declining aspen (<15% dieback) and white spruce. One circular plot (10-m radius) was established in each of these stands, giving a total of 12 plots for the study as a whole (Table 1).

Field Measurements and Sampling

In mid-September 1995, all trees within the 12 plots were numbered with aluminum tags, and the following information was recorded for each tree: species, diameter at 1.3 m height, and percentage crown dieback. Nearly all aspen crowns were still green, and leaf fall was negligible when these assessments were made. Stand basal area was determined from the diameters of living aspen in each of the 10-m radius (area of 314 m^2) plots.

Following the completion of leaf fall in mid-October 1995, one full-diameter increment core was obtained at 1.3 m height (random cardinal direction) from 10 or more aspen in each plot (where possible). The aspen were chosen to be representative of the range of diameters and degree of dieback in each plot. In addition, increment cores were obtained from a total of nine balsam poplar (*Populus balsamifera* L.) and 12 white spruce (four from each mixed wood stand). Each core was then placed in a labeled, 7-mm diameter drinking straw with its ends stapled. The height of each sampled tree was then measured using a Suunto clinometer. Aspen leaf litter from the current year's growing season was collected from within a 20-cm diameter area at five locations in each of the nine pure aspen plots (at the plot center and 5 m from the center in each cardinal direction). The litter was oven-dried (80°C) and the results expressed on an aerial basis (T/ha).

In late October 1995, disks (1.3-m height) were collected from at least five living aspen per plot, and from a total of 16 dead aspen, which could not be sampled using increment cores. In total, samples from 140 aspen stems (disks and/or increment cores) were obtained.

Sample Preparation and Ring Width Measurements

Increment cores and disks were oven-dried at 50°C. The cores were removed from straws, and mounted onto grooved boards with Franklin hide glue. Broken or fragmented cores were used, but only when they could be reassembled with confidence that no pieces were reversed or missing. The mounted cores were polished using a palm sander with the following grades of sandpaper: 120, 220, 320, 400, and 600. Disks were also sanded, beginning with coarse sandpaper (36, 60, and 80), and then polished using the same procedure as for cores.

Dating of rings was first conducted on the best material from each site, and then the poorest material (e.g., from dead or declining trees) was crossdated with known marker years. Ring widths were measured to within 0.025 mm using an ocular micrometer on a Zeiss compound dissecting microscope at 20× magnification, and data

Table 1. Aspen and mixed-wood stands used as sites for tree-ring analysis. All stands are located in the Bronson Forest near Highway 26, about 15–25 km north of St. Walburg, Saskatchewan (Saskatchewan forest inventory maps Z12 E62 N596 and Z12 E62 N595). Forest types are denoted as hardwood (H) or softwood (S) with estimated height in metres (20) and class of crown closure (B and C).

Site	Forest type	Stand no.	Number of plots
1	Aspen (H20C)	60	3
2	Aspen (H20C)	78	3
3	Aspen (H20C)	281	3
4	Aspen–white spruce (HS20B) mixed wood	15 (78)	1
5	Aspen–white spruce (HS20C) mixed wood	431	1
6	Aspen–white spruce (HS20C) mixed wood	11	1

were entered into a spreadsheet. Where possible, two radii per tree were measured to obtain mean ring width for each year. Tree rings that were abnormally pale in color (white rings caused by insect defoliation), or associated with fire scarring were noted. Selected sequences of tree rings from two representative disks were photographed after polishing them under a Wild M400 dissecting microscope with a Model MPS55 Photoautomat, using Ektachrome 64 ASA Tungsten film and a 200 watt halogen light source.

Tree-ring Analysis

Ring width measurements in millimetres were used to estimate annual values of basal area increment (in square centimetres) for each tree, as follows: First, the annual tree ring measurements were expressed as a cumulative distance (in millimetres) from the center of the tree. For increment cores not including the center, the distance to the first visible ring was estimated using concentric circles printed on a transparent overlay. Basal area increment for a given year was then calculated as:

$$3.1416\ (r_y^2 - r_{y-1}^2)$$

where r_y and r_{y-1} are the radii (cumulative distance to center in centimetres) at the end of that year (y) and the previous year (y-1), respectively.

Annual basal area increments for the aspen in each plot were then averaged to obtain the average area increment per stem. In a few instances, aspen were excluded from the plot average, if the degree of crown dieback was markedly atypical for the decline class being represented (e.g., trees belonging to adjacent clones).

Live Aboveground Biomass

The quantity of living, aboveground biomass in each pure aspen plot was estimated from diameters and tree heights using the following equation for aspen given by Singh (1982):

$$W = 0.3496 + 0.01916\ D^2 H$$

where W is ovendry, aboveground biomass (in kilograms) excluding foliage, D is stem diameter (in centimetres) at 1.3-m height, and H is total tree height (in metres). Heights of trees not measured were estimated by linear regression of $\log_e$-transformed heights and diameters of those trees whose heights were measured (N = 82). In the calculations, the quantity of living (i.e., functional) stem biomass was assumed to be proportional to the percentage of live crown remaining in each tree.

Table 2. Climate stations used to estimate historic weather conditions for the Bronson Forest. Mean annual precipitation and temperature, and mean July temperature for the period 1951–1980 are shown (Environment Canada 1982). Turtleford and Waseca were used only when no data were available from the first four stations.

Station	Location	Altitude (m)	Periods covered	Mean annual precip. (mm)	Mean annual temp. (°C)	Mean July temp. (°C)
St. Walburg	53°43'N 109°09'W	663	1918–1955 1957–1973 1983–1994	419	0.1	16.2
Loon Lake	54°03'N 109°06'W	543	1930–1946 1951–1955	428	0.6	16.6
Spruce Lake	53°32'N 109°05'W	604	1956–1971	419	0.4	16.4
Butte St. Pierre	53°27'N 109°12'W	533	1955–1995	390	0.1	16.2
Turtleford	53°27'N 109°00'W	587	1920–1970	401	0.7	16.8
Waseca	53°06'N 109°30'W	648	1907–1995	449	1.0	16.8

Weather Data

Daily maximum and minimum temperature, and daily precipitation (rain plus snow water equivalent) were obtained from Environment Canada (1982) for six climate stations (Table 2). Four of these (St. Walburg, Loon Lake, Spruce Lake, and Butte St. Pierre) are located within 40 km of the Bronson Forest study area. No single station, however, was operating continuously over the period of interest (1918–1995), and missing data were commonly encountered. Thus, historic weather in the Bronson Forest was determined using a computer program as follows: 1) for each day, if data were available from one or more of the stations within 40 km, then the average of these was used; 2) if no data were available, then Turtleford data (located about 50 km to the southeast) were used; 3) if Turtleford data were also missing, then Waseca (located about 75 km to the south) data were used. The Waseca data were needed only for a few periods (up to 1 month) prior to 1931. Merging of these data sets should introduce very minor biases into the climate record because all stations had similar long-term climate normals. From the daily data set for the Bronson Forest, monthly averages of daily maximum and minimum temperatures and total monthly precipitation were also determined.

Calculation of the Annual Climate Moisture Index (CMI)

Yearly changes in moisture were assessed using a climate moisture index (CMI) developed by Hogg (1997). The CMI was based on the quantity P minus PET, where P is the annual precipitation and PET is the annual potential evapotranspiration (i.e., expected loss of water vapor loss from the landscape under well-watered conditions) using a simplified form of the Penman-Monteith equation. In general, negative values of the CMI denote dry conditions typical of the aspen parkland, whereas positive values indicate levels of moisture that are normally associated with the boreal forest (Hogg 1994; Hogg 1997).

The PET was calculated from vapor pressure deficit, which was in turn estimated from the average daily maximum and minimum temperature for each month. Precipitation that falls late during a calendar year (e.g., October–December) cannot have an effect on tree growth during that year. Thus in the analyses of growth in relation to moisture, the CMI was calculated using several different 12-month periods (1 July to 30 June, 1 August to 31 July, 1 September to 31 August, and 1 October to 30 September). The period giving the best relationship between tree growth and the CMI was then used in the subsequent analyses that included other factors.

Data Sources on Insect Defoliation Events

The spatial coverage of insect defoliation events across Canada were mapped and reported annually for the period since 1937 by the CFS Forest Insect and Disease Survey unit. The more recent records for the prairie provinces are provided in the CFS Information Report series, published by the Northern Forestry Centre in Edmonton. More detailed records, including original sketch maps showing the extent of forest tent caterpillar outbreaks in the Bronson Forest, were made available for this study by James Brandt, Forest Health Unit Leader at the Northern Forestry Centre. This information was used to verify that the white tree rings observed in aspen cores and disks corresponded to years when defoliation by forest tent caterpillar was recorded.

Regression Modeling

Preliminary analyses of climatic trends over time (1919–1995) in the Bronson Forest were conducted using simple linear regression. A dynamic regression approach using Forecast Pro software (Business Forecast Systems, Inc.) was used to examine the combined influences of climatic factors and insect defoliation events on aspen growth for the period from 1950–1995. Dynamic regression is similar to multiple regression but has the added capability to include time-lagged variables and autoregressive error terms in the regression model. The variable describing insect defoliation intensity each year was determined based on the proportion of trees having white rings for each year. The climatic variables examined included the CMI, annual precipitation (water year defined as for the CMI), growing degree days, and a summer frost index. Growing degree days were calculated as the annual cumulative sum of mean daily temperatures above 5°C. The summer frost index was calculated as the sum of squares of daily deviations of minimum temperature from 0°C beginning on the date of aspen leafout and ending on 31 August. The date of leafout was assumed to occur when the number of growing degree days had reached 120 (Hogg 1999). A similar analysis was conducted on white spruce chronologies obtained from the mixed wood stands.

Based on the above analyses of aspen growth, the best fit of basal area increment versus climate and defoliation was obtained. Different scenarios were then examined by eliminating defoliation and/or drought from the dynamic regression equation.

RESULTS AND DISCUSSION

Stand Characteristics in Sites and Decline Classes

Examples of the general appearance of pure aspen stands in the three classes of decline are shown in Figure 1. Trees in healthy stands showed little or no evidence of dieback; in the light-decline class, trees frequently had dead branches protruding up to several metres above their live crowns; while in the heavy-decline class, most trees were either dead or had experienced severe crown dieback.

Table 3 gives a summary of the characteristics of aspen stems sampled in each site. In the heavy decline class, 16 of the 31 trees sampled had died but were still standing when sampled, with the last growth ring occurring between 1989 and 1995. Average crown dieback within each class was 75% (heavy decline), 29% (light decline), 1% (healthy pure aspen stands), and 3% (mixed wood stands).

Average heights ranged between 14 and 18 m, and did not vary significantly among the different stand classes. Average stem diameter (diameter breast height, DBH) was generally lower in the heavy decline class (15.8 cm) than in the other classes (17–19 cm), presumably reflecting the reduced radial growth of aspen in the heavily declining stands.

Mean stand age in all classes ranged from 57 to 63 years, based on dating of disks and increment cores that included the center ring. This indicates that the aspen stands mostly originated

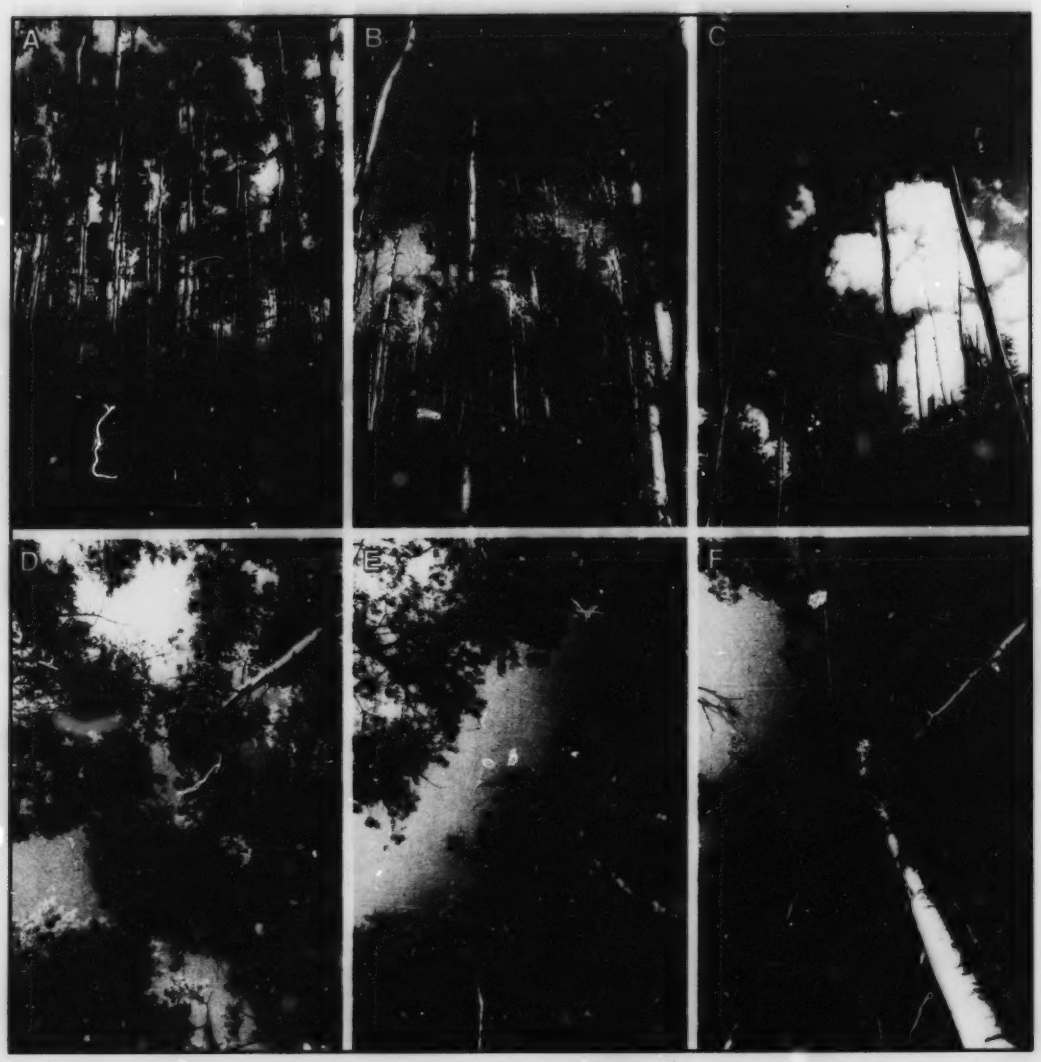

Figure 1. Pure aspen stands in various stages of decline in the Bronson Forest in September 1995. Healthy **(A, D)**, light decline **(B, E)**, and heavy decline **(C, F)**.

Table 3. Characteristics of trembling aspen sampled for tree-ring analysis. A) characterisics by decline class and site; B) summaries grouped by decline class, by site, and overall characteristics of trees sampled in pure aspen versus mixed wood stands. The DBH is stem diameter at breast height (1.3 m). Heights of trees with broken crowns were excluded. Tree ages are based on cores or disks collected at 1.3 m height in October 1995 (cores or disks that could not be dated are excluded).

Class	Site no.	Aspen sampled	No. dead	DBH (cm) Mean (Range)	Height (m) Mean (Range)	Crown dieback (%) Mean (Range)	Age in 1995 (years at BH[a]) Mean (Range)
A)							
Heavy	1	10	3	14.0 (12–16)	15.5 (14–17)	68 (40–100)	56 (53–57)
Heavy	2	10	5	16.7 (12–22)	16.0 (14–18)	75 (35–100)	62 (52–66)
Heavy	3	11	8	16.6 (14–19)	15.6 (15–16)	83 (30–100)	63 (61–64)
Light	1	9	0	18.1 (12–24)	13.8 (11–16)	28 (15–50)	55 (51–57)
Light	2	11	0	15.6 (13–20)	15.7 (14–17)	29 (10–50)	62 (51–65)
Light	3	11	0	19.3 (15–25)	17.8 (17–19)	30 (15–50)	60 (49–65)
Healthy	1	13	0	18.0 (14–22)	15.5 (12–17)	2 (0–10)	49 (46–51)
Healthy	2	12	0	16.3 (13–21)	15.8 (14–18)	1 (0–10)	64 (62–65)
Healthy	3	15	0	19.5 (14–31)	17.7 (13–21)	1 (0–15)	58 (46–65)
Mixed wood	4	13	0	19.0 (14–28)	16.8 (15–18)	2 (0–10)	70 (67–72)
Mixed wood	5	13	0	17.7 (13–21)	14.2 (11–16)	1 (0–10)	55 (49–57)
Mixed wood	6	10	0	20.1 (13–26)	15.0 (12–17)	6 (0–30)	64 (61–66)
B)							
Heavy	1–3	31	16	15.8 (12–22)	15.7 (14–18)	75 (30–100)	60 (52–66)
Light	1–3	31	0	17.7 (12–25)	15.8 (11–19)	29 (10–50)	59 (49–65)
Healthy	1–3	40	0	17.9 (13–31)	16.3 (12–21)	1 (0–15)	57 (46–65)
All classes	1	32	3	16.7 (12–24)	14.9 (11–17)	33 (0–100)	53 (45–57)
All classes	2	33	5	16.2 (12–22)	15.8 (14–18)	35 (0–100)	63 (51–66)
All classes	3	37	8	18.5 (14–31)	17.0 (13–21)	38 (0–100)	60 (46–65)
Pure stands	1–3	102	16	17.1 (12–31)	15.9 (11–21)	35 (0–100)	59 (46–66)
Mixed wood	4–6	36	0	18.9 (13–28)	15.3 (11–18)	3 (0–30)	63 (49–72)

[a] BH = breast height.

from about 1930 (1.3 m tall in the mid-1930s). The aspen sampled at sites 1 and 5 were generally younger than average (49–56 years), whereas aspen at mixed wood site 4 were older than average (70 years).

Live basal area, aboveground biomass, and leaf-litter fall in the heavy decline class were all less than half as great as in the healthy class, while the light decline class generally showed values intermediate between healthy and heavy decline (Table 4). Mean leaf area index was estimated at 2.7, 2.2, and 1.1 for the healthy, light decline, and heavy decline classes, respectively, based on the observed values of litter fall and assuming a specific leaf area of 11.5 m^2/kg for

Table 4. Estimated live basal area, stem density, aboveground biomass, and leaf-litter fall in 1995 for aspen within the 9 circular sampling plots of 10-m radius in pure stands. A) by decline class and site, and B) summaries grouped by decline class.

Class	Site no.	Live basal area (m^2/ha)	Live density (stems/ha)	Aboveground biomass (T/ha)	Leaf-litter fall in 1995 (T/ha)
A)					
Heavy	1	10.3	668	29	0.90
Heavy	2	13.8	637	42	1.12
Heavy	3	12.7	541	44	0.90
Light	1	15.7	700	49	1.57
Light	2	16.7	859	52	2.02
Light	3	21.7	700	68	2.13
Healthy	1	17.4	891	67	2.77
Healthy	2	30.1	1369	113	2.34
Healthy	3	29.0	1241	114	1.91
B)					
Heavy	1–3	12.3	615	38	0.97
Light	1–3	18.0	753	56	1.91
Healthy	1–3	25.5	1167	98	2.34

aspen leaf litter (E.H. Hogg, unpublished data). This indicates that the photosynthetic capacity of the aspen canopy as a whole in 1995 was greatly reduced in the declining stands, particularly those in the heavy decline class.

Fire History

Maps of fire history for the study area (Roger Nesdoly, Mistik Management Ltd., personal communication, November 1995) indicate that much of the area burned during the severe fire seasons of 1948 and 1949. However, all of the aspen sampled in this study would have been present in 1948 (minimum age of 46 years at 1.3 m in 1995; Table 3). Indeed, several of the aspen sampled had fire scars that dated to the 1948–1949 period.

All stands sampled were classed on the forest inventory maps as H20C, HS20B, or HS20C (Table 1), whereas a large fraction of the other aspen stands in the area are in the H15C or H15D category. This indicates that the aspen stands included in this study might be older (20 m height) than those in many adjacent aspen stands (15 m height), and the latter might have originated from the 1948–1949 fires. These fires probably destroyed some stands, but the sites sampled experienced low-intensity ground fires only, thus escaping major damage. It is also likely that the Bronson Forest was affected by the great fires of 1919 (Peter Murphy, Professor Emeritus, Department of Renewable Resources, University of Alberta, personal communication, January 1999), but few detailed records are available to determine which parts of the study area might have been affected.

Climate Trends from 1918 to 1995

Trends in climatic characteristics are shown in Figure 2, for the period 1918–1995. Regression analyses indicate that the mean temperature in the Bronson Forest has warmed significantly by about 1.5°C since 1918 (Fig. 2a, Table 5). This is similar to the 1.4°C of warming that has been reported over the past century for the western boreal forest as a whole (Environment Canada 1995). It is interesting to note, however, that

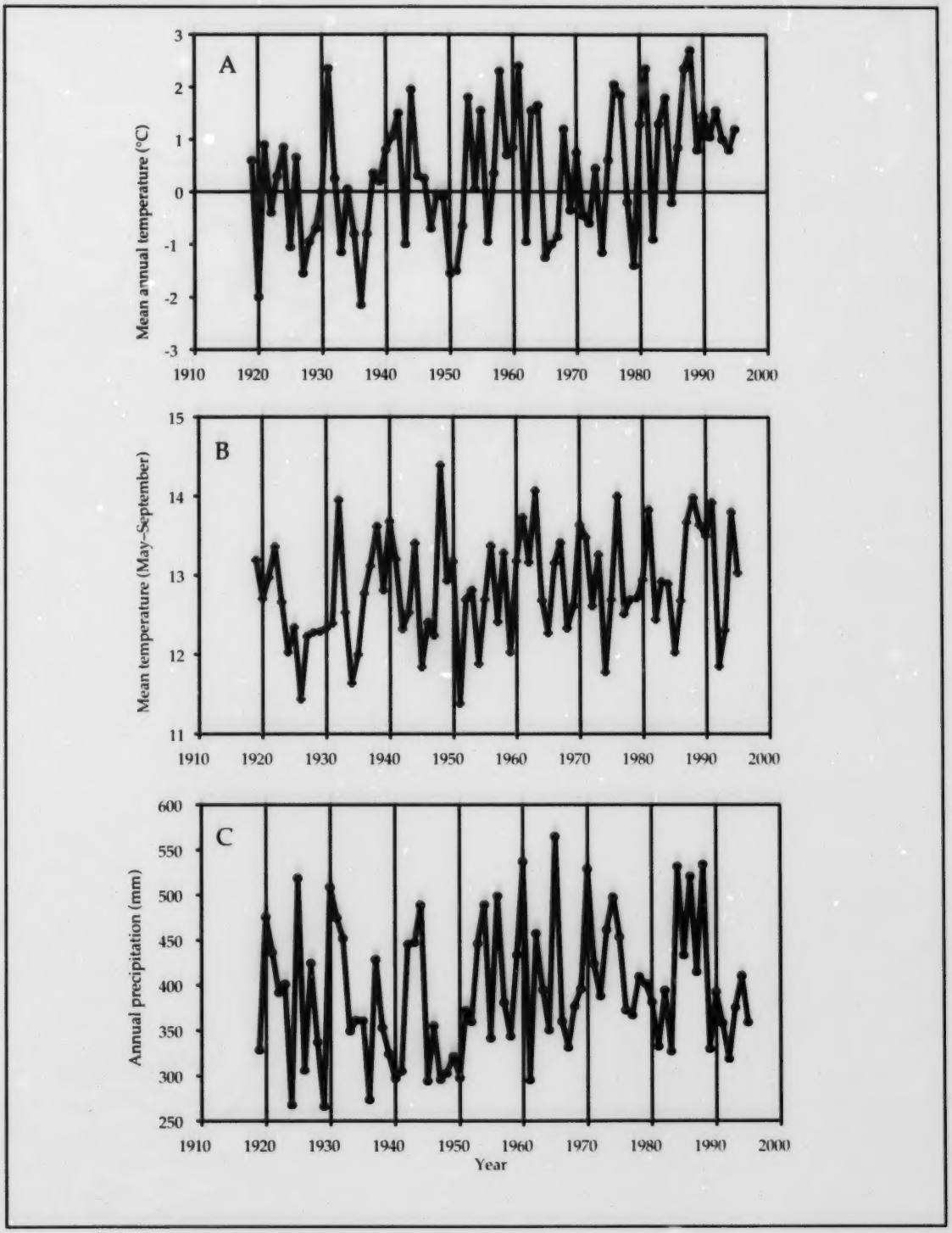

Figure 2. **Trends in climatic factors for the Bronson Forest, 1919–1995. A)** annual temperature; **B)** growing season temperature; and **C)** annual precipitation.

Table 5. Regression analysis of climate trends in the Bronson Forest, for the period from 1918 to 1995. The independent variable Y indicates the number of years since 1918. Statistical significance of trend is also shown.

Regression equation	Estimated change 1918–1995	Statistical significance
Mean annual temperature = –0.4°C + 0.019° × Y	+1.5°C	P<0.01
Mean annual daily maximum temperature = 6.8°C + 0.005° × Y	+0.4°C	NS[a]
Mean annual daily minimum temperature = –7.6°C + 0.033° × Y	+2.5°C	P<0.001
Mean temperature (May–Sept.) = 12.5°C + 0.008° × Y	+0.6°C	P<0.05
Mean daily maximum temperature (May–Sept.) = 20.7°C – 0.010° × Y	–0.8°C	NS
Mean daily minimum temperature (May–Sept.) = 4.4°C + 0.025° × Y	+2.0°C	P<0.001
Mean annual precipitation (Sept.–Aug.) = 375 mm + 0.47 mm × Y	+36 mm	NS
Mean growing season precipitation (May–Sept.) = 249 mm + 0.51 mm × Y	+39 mm	NS
Climate moisture index (Sept.–Aug.) = –13.5 + 0.10 × Y	+7.4	NS

[a] NS = not significant (P > 0.05).

nearly all the warming can be attributed to increases in nighttime (daily minimum) temperatures. Similar patterns are seen in the temperature trends based on the growing season only (May to September, Fig. 2b).

Precipitation also showed a slight tendency to increase slightly over the period 1918–1995 (Fig. 2c), although the trends were not statistically significant, either on an annual or growing season basis (Table 5).

Changes in the climate moisture index (CMI) from 1919 to 1995 (water year from September 1 to August 31) are shown in Figure 3. There was a tendency for an increase in CMI over time (indicating moister conditions), but the trend was not statistically significant (Table 5). Based on the CMI, the two driest years on record were 1948–1949 and 1949–1950, which coincide with the timing of the most recent major fires in the study area.

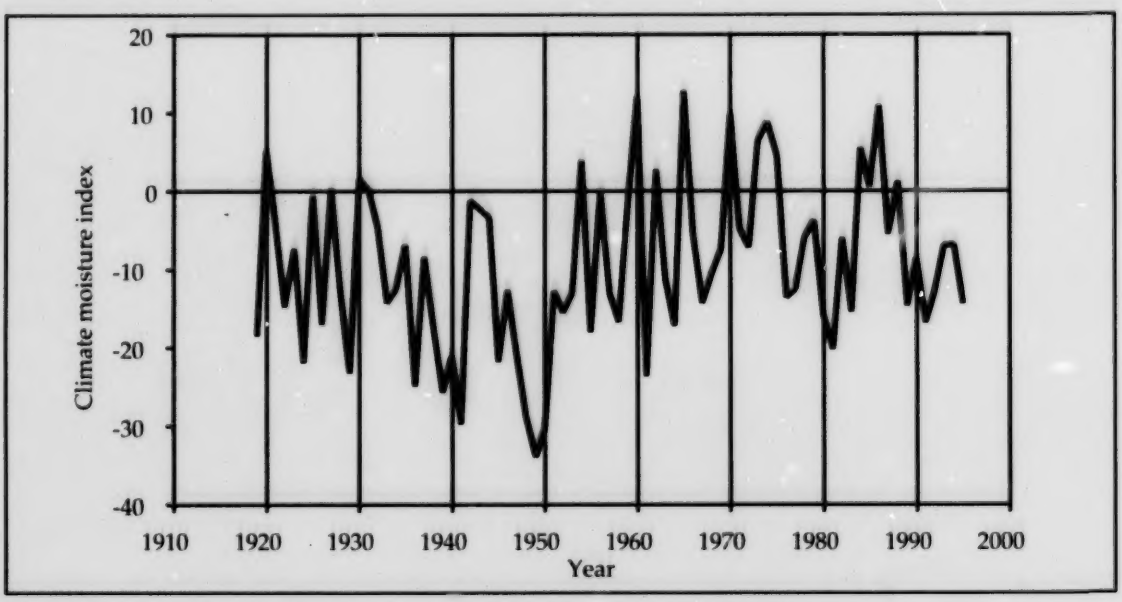

Figure 3. Trends in the climate moisture index for the Bronson Forest.

Recent Climate (1960–1995)

In many areas on the Canadian prairies, the drought experienced in the 1980s was comparable in severity to that of the 1930s. In the Bronson Forest, however, the 1980s appeared to be slightly wetter than the long-term average, based on precipitation amounts (Fig. 2c) or the climate moisture index (Fig. 3). The three driest years since 1951 were recorded in 1963–1964, 1979–1980 and 1994–1995, but based on the CMI, these were not as severe as earlier droughts in 1939–1941 and 1948–1949. Although there has been an absence of very wet years since 1986, the data would suggest that climatic conditions have been generally moister since 1960 than during the preceding period (1930–1960). It should be noted, however, that earlier rain gauge designs were less reliable and tended to underestimate total precipitation amounts by 7% or more (Metcalfe et al. 1997).

The most striking evidence of recent climatic change is in the records of temperature (Fig. 2a). Mean temperature was well above the long-term average every year from 1987 to 1995, mainly due to warmer than normal winters and springs. In March 1992, the mean monthly temperature (–1.6°C) was about 7°C greater than average, making this the warmest March on record (period 1919–1995), while March 1993 (mean temperature of –3.2°C) was the second warmest.

White Growth Rings and Insect Defoliation History

During the course of tree-ring measurements, white growth rings were encountered in all 138 aspen that were sampled. Unlike the light-colored rings that have been reported in conifers (e.g., Volney and Mallett 1992; Szeicz 1996; Liang et al. 1997), the appearance of both early and latewood xylem in the white rings of aspen differed dramatically from that in normal growth rings (Fig. 4).

White rings were most common during two major periods: 1962–1965, and 1978–1990 (Tables 6 and 7). The timing of white ring formation was generally similar among all sites, although there were instances where white rings were recorded in only one site in a given year (e.g., 1978, site 4 only; 1983, site 3 only). Isolated occurrences of white rings were also noted in 1949, 1953, and 1956 (Table 6).

There was generally a good correspondence between the presence of white rings and the recorded history of defoliation by forest tent caterpillar, based on the records of the CFS Forest Insect and Disease Survey (Table 7). All 3 years during the period 1962–1964 had a high frequency of white rings in some or all (1964) of the stands, coinciding with the same 3 years when extensive defoliation was recorded. The recorded history of outbreaks from 1978 to 1990 also corresponded well with the presence of white rings, except in 1985–86, when white rings were abundant but the only recorded outbreak in the vicinity was located about 30 km west of the study area. It should be noted, however, that defoliation mapping by the Forest Insect and Disease Survey is conducted at a very large geographic scale (the three prairie provinces and Northwest Territories), and thus it is likely that some localized areas of defoliation are missed by the surveys in a given year.

The suggestion that white rings are caused by insect defoliation events is further supported by the complete absence of white rings in all of the 138 aspen stems sampled, for the periods 1966–1977 and 1993–1995, when no defoliation outbreaks were recorded during the regional surveys. The sporadic occurrence of white rings in 1949 and 1956 may have been caused by another insect defoliator, the large aspen tortrix (*Choristoneura conflictana* [Walker]), which was recorded near the study area by the Forest Insect and Disease Survey during those years. The white rings noted at one of the sites in 1953 were probably associated with a major outbreak of forest tent caterpillar immediately to the east of the study area during that year.

If it is assumed that white rings are formed only during years with insect defoliation, the proportion of trees with white rings (Table 7) can be used as an index of defoliation intensity in each stand class, or for pure stands as a whole (bold type). Based on this assumption, the years with the greatest defoliation intensity by forest tent caterpillar were 1964, 1980, and three consecutive years from 1986 to 1988.

Within each class, the average number of defoliation years per tree can also be estimated by adding the annual proportion of white rings across the period of interest. Using this approach, aspen stems in the heavy decline stands were

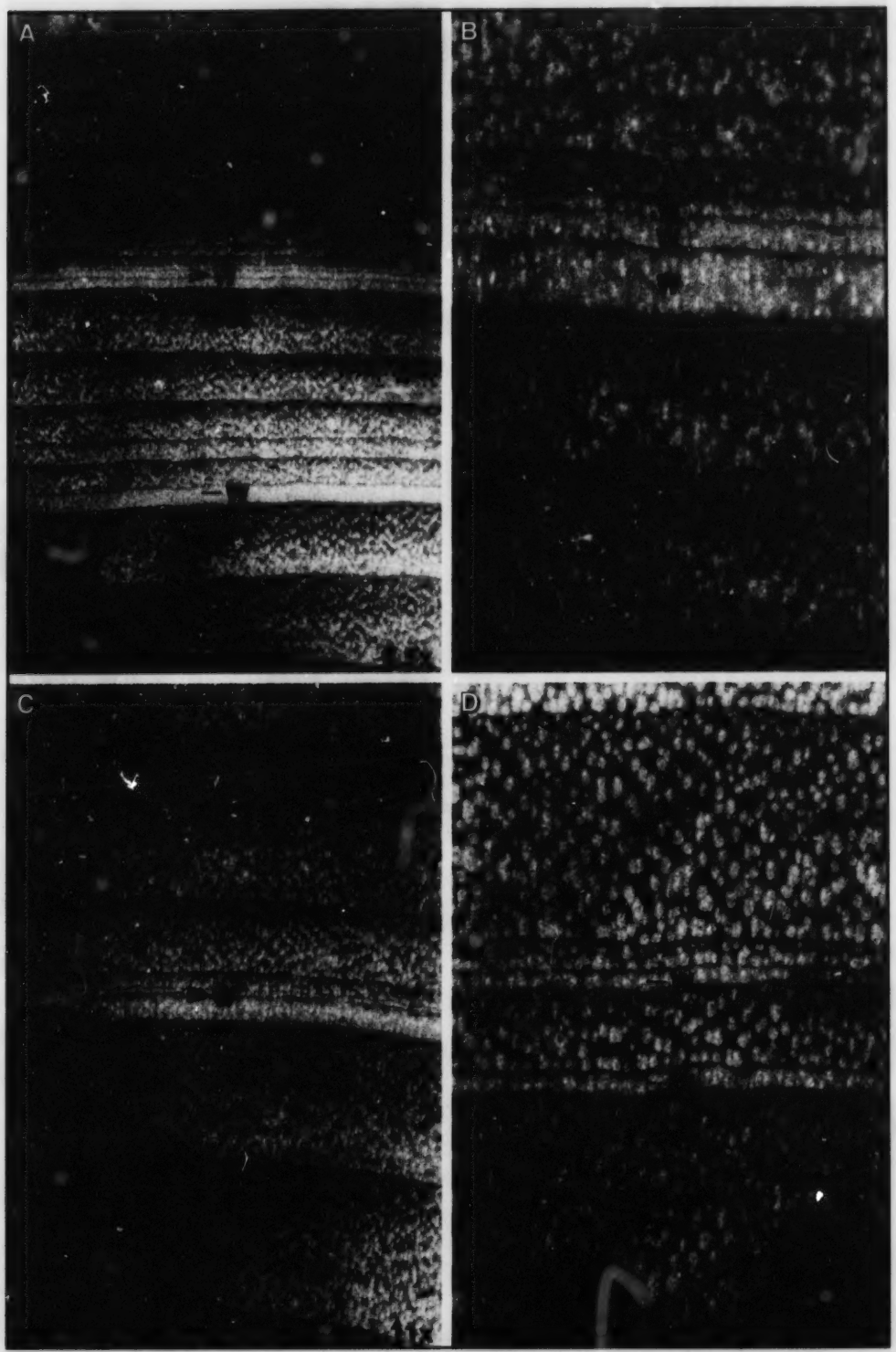

Figure 4. Tree rings from aspen in the Bronson Forest, showing white rings (W) and interannual variation in radial growth. Disks were collected in October 1995 from healthy, 20-cm diameter aspen: **A)** tree no. 331, 1978–1995; **B)** tree no. 331, 1984–1990; **C)** tree no. 331, 1961–1967; **D)** tree no. 67, 1984–1989.

Table 6. Tree-ring analysis data with years showing white colored rings, which are typically associated with insect defoliation

	Heavy decline			Light decline			Healthy			Mixed wood		
Year	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6
1992									*			
1991												
1990	*		**									
1989	**	*	*		*					*		
1988	**	**	***	***	**	***	**	***	**	**	***	***
1987	**	***	***	**	***	***	***	***	***	***	***	***
1986	**	***	***		***	***		***	***	***	***	**
1985	***	**	*	***			***					
1984												
1983			***			*						
1982	***		***	*		**	**					
1981										*		
1980	***	***	***	***	***	***	***	***	***	***	***	***
1979		**			**			*		***		
1978										**		
1965	*						*					
1964	***	***	***	**	***	***	***	***	***	***	*	***
1963	***		***	***		**	***		***		*	
1962	**		***			*	**				*	
1956		*			*			**		*		*
1953										**		
1949						**		*		**		
Mean no. white rings												
1978–1992	4.5	4.2	6.1	3.1	3.8	4.3	3.8	4.0	3.3	4.5	3.3	3.4
1962–1965	2.2	0.9	2.5	1.0	1.0	1.5	2.4	1.0	1.6	1.0	0.3	1.0

Note: Asterisks show proportion of stems affected in each combination of site and decline class (pure aspen stands only): *** = 80–100% of stems affected; ** = 20–79% of stems affected; * = 1–19% of stems affected.

defoliated for an average of 5.0 years for the period 1978–1990, compared to 3.7–3.8 years in the light decline and healthy classes of pure stands and mixed wood stands (Table 7). However, because of high variation in the number of white rings among the three sites (Table 6), no differences could be detected statistically (two-factor ANOVA, $P>0.10$). Similarly, the mean number of white rings during the period 1962–1965 averaged slightly higher in the heavy decline class (1.9) compared to the other classes (0.8–1.7), but the differences were not statistically significant. Thus it is possible that differences in defoliation intensity contributed to the observed differences in crown dieback among the aspen clones sampled, but a larger number of sites would need to be sampled to confirm this.

Table 7. Percentage of aspen stems with white rings in each decline class of pure stands (sites 1–3), and in mixed-wood stands (sites 4–6), based on tree-ring analysis

	Pure stands				Mixed stands	
Year	Heavy decline Sites 1–3	Light decline Sites 1–3	Healthy Sites 1–3	Mean Sites 1–3	Mean Sites 4–6	Records of insect defoliation
1992	0	0	2	1	0	Not recorded in study area
1991	0	0	0	**0**	0	Not recorded in study area
1990	23	0	0	**8**	0	Isolated FTC S of St. Walburg
1989	16	3	0	**6**	5	FTC regionally, rare in study area
1988	52	68	73	**64**	55	Extensive FTC defoliation
1987	84	71	90	**82**	87	FTC defoliation in study area
1986	74	65	68	**69**	92	FTC recorded 30 km to west
1985	48	29	33	**37**	0	FTC recorded 30 km to west
1984	0	0	0	**0**	0	Not recorded in study area
1983	29	6	0	**12**	0	Not recorded in study area
1982	61	19	13	**31**	0	Isolated FTC near St. Walburg
1981	0	3	0	**1**	5	Isolated FTC in study area
1980	100	100	90	**97**	92	Extensive FTC defoliation
1979	10	13	3	**9**	32	FTC in E part of study area
1978	0	0	0	**0**	8	Not recorded in study area
1965	3	0	3	**2**	0	Isolated, localized FTC
1964	87	81	93	**87**	68	Extensive FTC defoliation
1963	58	39	60	**52**	3	Extensive FTC defoliation
1962	42	3	13	**19**	5	Extensive FTC defoliation
1961	0	0	0	**0**	0	Isolated, localized FTC
Mean no. white rings						
1978–1992	5.0	3.8	3.7	**4.2**	3.8	
1962–1965	1.9	1.2	1.7	**1.6**	0.8	

Note: Number of trees sampled in each class is shown in Table 3 (missing rings not included in percentages). Also shown is the extent of insect defoliation by forest tent caterpillar (FTC) in the study area, based on records and maps from the Canadian Forest Service Forest Insect and Disease Survey (James Brandt personal communication, see also Brandt 1995).

Tree-ring Analysis of Aspen Growth in Pure Stands by Decline Class

Figure 5 shows the mean annual increase in basal area for aspen in the three decline classes during the period 1930–1995 (average of sites 1, 2, and 3). In general, aspen growth in the heavy, light, and healthy stands was very similar prior to 1965. From 1930 to 1950, basal area increment showed a gradual increase, which is the typical pattern during the first 15–20 years of growth (when even wide rings result in small basal area increments because of the small stem diameter).

There was a dramatic reduction in aspen growth for all decline classes during the period 1961–1964 (Fig. 5), which coincides with a period of intense defoliation by forest tent caterpillar (Table 7), coupled with drier than normal weather

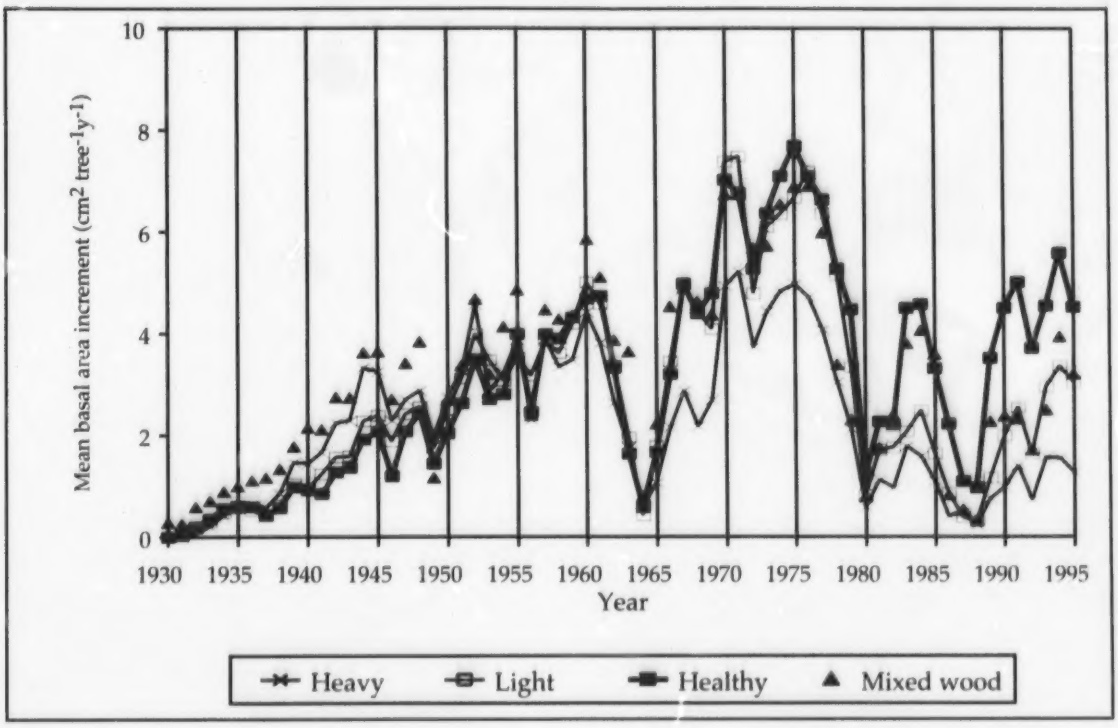

Figure 5. Average growth of aspen by decline class and stand type, based on dendrochronology.

conditions in 1961 and 1964 (Fig. 3). Following 1964, the aspen in all classes recovered, but average growth in the heavy decline stands was consistently less than in the light decline and healthy stands.

The best growth was observed during the 1970s, but in the 1980s there were two major collapses in growth, each associated with periods of defoliation by forest tent caterpillar (1978–1983, and 1985–1990). Following 1980 (a year with both drought and intense defoliation), there was a clear separation in growth among the three decline classes, which continued until the trees were sampled in 1995.

In the 1990s, growth in the healthy and light decline stands were both showing good recovery, although the recovery was slower in the light decline class. In the heavy decline class, however, growth remained poor and high stem mortality was continuing to occur (5 of the 16 dead trees sampled had died in 1995).

It should be noted that there were also differences among the three sites, as shown in Figure 6. In general, the annual basal area increment was smallest in site 2, and at this site the heavy and light decline stands showed very similar rates of recent growth.

Tree-ring Analysis of Aspen Growth in Mixed-wood Stands

Initially, it had been postulated that aspen growing in mixed stands were impacted less by forest tent caterpillar, and thus could serve as controls in this study of aspen decline. However, the average number of white rings (1978–1992) was nearly the same in the mixed wood and pure healthy stands, thus providing no support for this hypothesis (Table 7).

In terms of basal area increment, the tree-ring analysis (Fig. 5) showed that after 1985, average growth of mixed wood aspen was reduced,

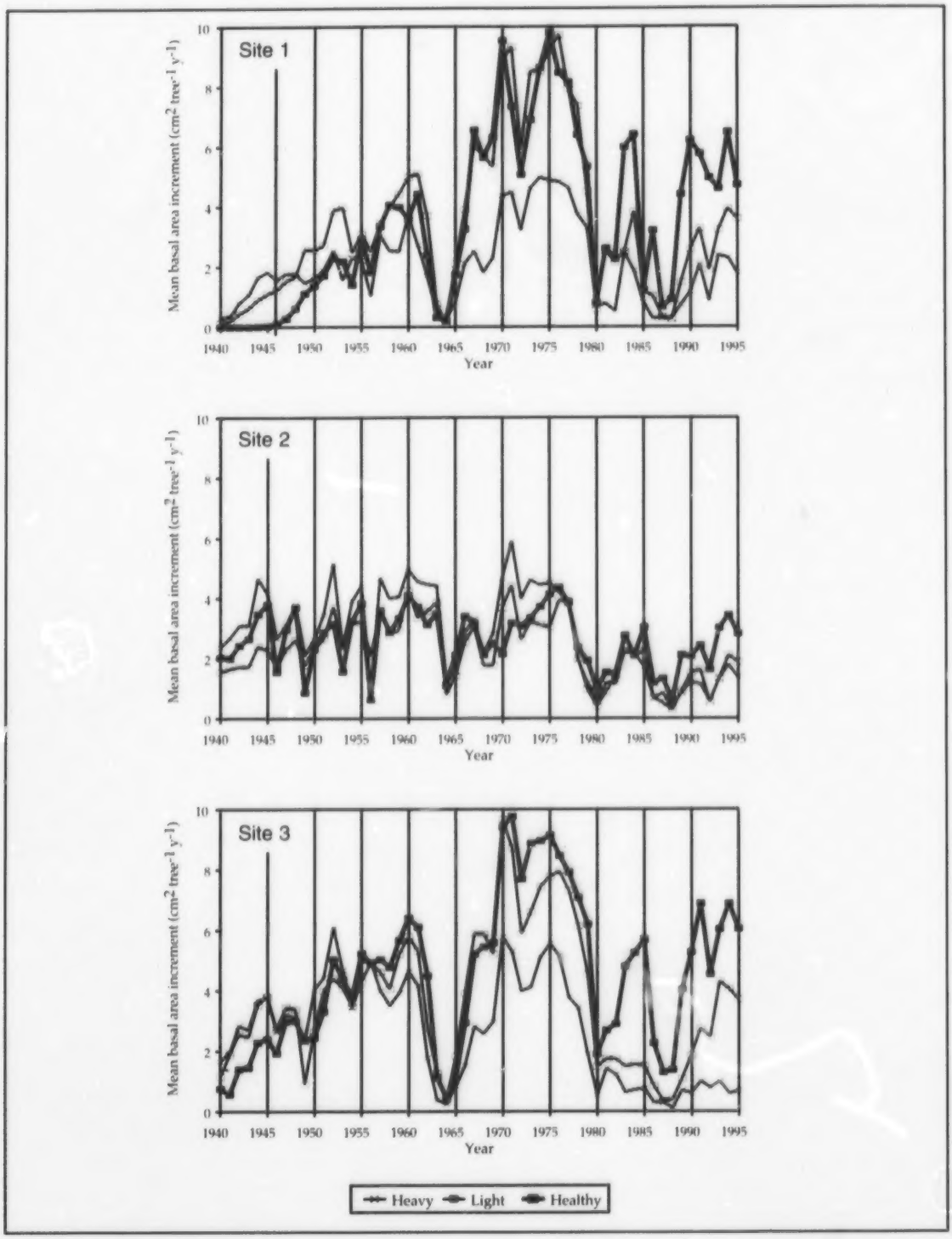

Figure 6. Average growth of aspen by site and decline class in pure stands, based on dendrochronology (sites 1, 2, and 3).

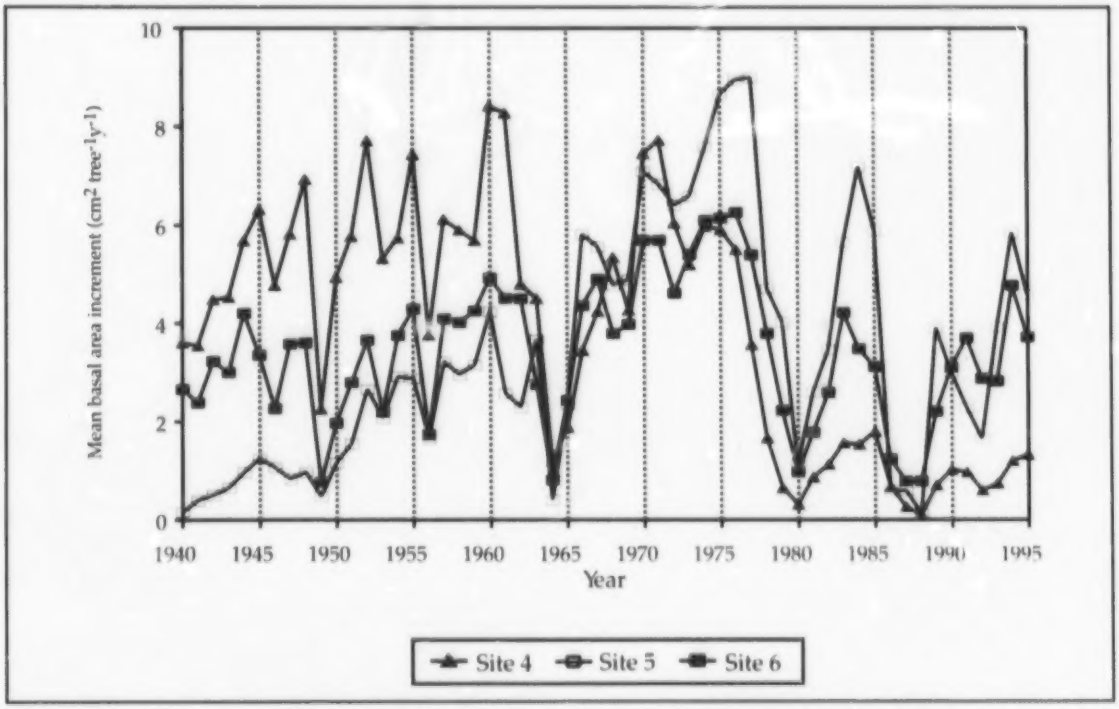

Figure 7. Average growth of aspen by site in mixed-wood stands, based on dendrochronology (sites 4, 5, and 6).

relative to the healthy sites in pure aspen stands. Indeed, the average growth of aspen in the mixed wood stands more closely resembled that in the lightly declining pure stands during this period, despite the absence of aspen dieback in the mixed wood stands.

As with the pure aspen stands, there were differences in growth responses among the three mixed wood sites (Fig. 7). At site 4, where aspen were oldest (Table 3), the early growth prior to 1964 was considerably higher than in sites 5 and 6. However, growth in site 4 was dramatically reduced in the late 1970s, and thereafter remained much lower than in the other sites.

Growth Trends of Balsam Poplar

Several balsam poplar were sampled for purposes of comparison with aspen, because it was initially expected that this species would be less prone to defoliation by forest tent caterpillar. The balsam poplar sampled were generally smaller in diameter (about 13 cm) and height (about 12 m) than the aspen, but were of similar age.

Surprisingly, the overall pattern of balsam poplar growth was very similar to that of aspen (Fig. 8). An analysis of white rings in the nine balsam poplar sampled indicated that from 1962 to 1990, this species was defoliated almost as frequently (average of 3.9 years) as aspen (average of 5.4 years for all stands). Thus it was not possible to use the balsam poplar as a control for aspen growth during years of defoliation. Although egg bands of forest tent caterpillar are rarely found on balsam poplar, the larger instars do migrate to adjacent trees during outbreaks and thus also defoliate this tree species (John Spence, Department of Biological Sciences, University of Alberta, personal communication, February 1997).

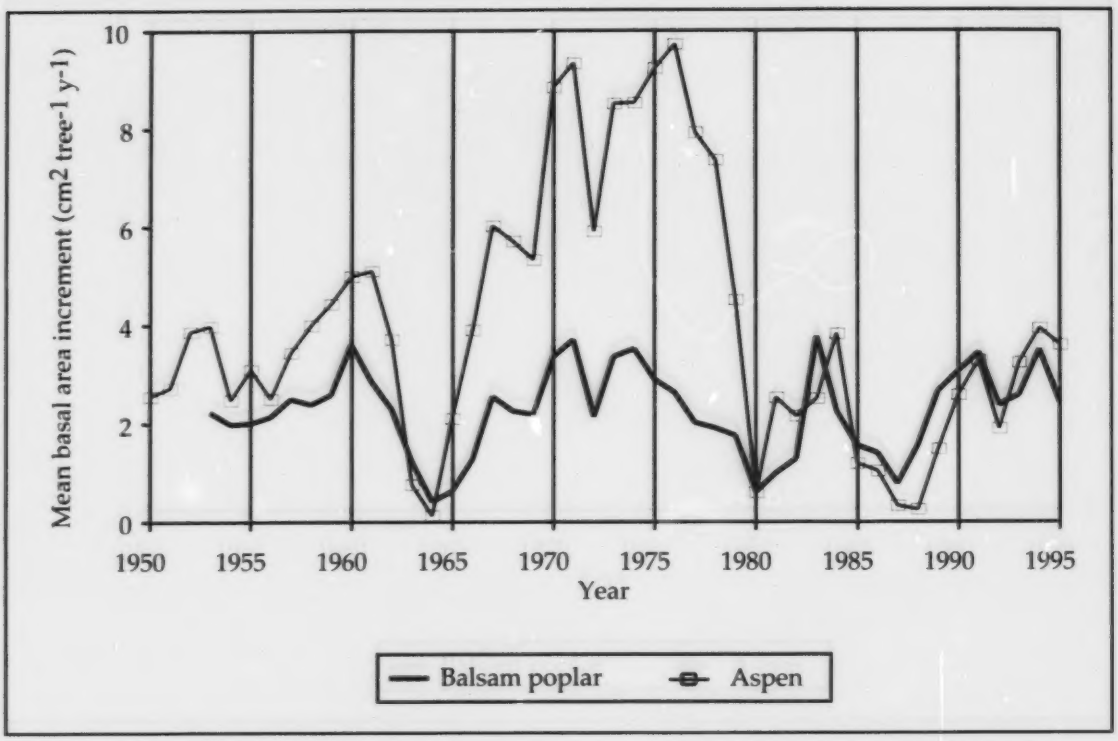

Figure 8. **Average growth of 5 balsam poplar and 9 aspen at site 1, light decline class, based on dendrochronology.**

Growth Trends of White Spruce in Mixed-wood Stands

Cores were collected from four white spruce in each of the three mixed wood stands (sites 4–6); characteristics of the trees sampled are given in Table 8. The largest white spruce were encountered at site 5, where the average estimated age of the four trees sampled was 83 years. The mean basal area increment of the white spruce in these mixed wood stands is shown in Figure 9, along with that of the 38 aspen at the same sites. It is interesting to note that basal area increment of the white spruce was much greater than in the aspen, especially over the period since 1980. Furthermore, there was almost no relationship between the patterns of white spruce and aspen growth over time ($r^2 = 0.04$). The greatest growth of spruce was recorded in the late 1980s, during a period of extremely poor growth of the aspen. However, the white spruce showed a more pronounced reduction in growth than the aspen in 1995.

Statistical Modeling of Aspen Responses to Climate and Defoliation

Dynamic regression analysis was used to examine relationships between aspen growth, climatic conditions, and defoliation by forest tent caterpillar. The period chosen for the analysis was from 1950 to 1995: earlier data were not included to avoid possible confounding effects of the 1948–1949 fires, juvenile growth, and missing early data from increment cores.

The dependent variable for this analysis (TA_GROWTH) was calculated for each year as the average basal area increment (square centimetres per tree). Averages of basal area increment for all aspen in the three pure stands were used (102 trees in all decline classes of sites 1, 2, and 3, Fig. 6).

The following independent variables were used:

Table 8. Characteristics of white spruce in mixed wood stands, sampled for tree-ring analysis. DBH is stem diameter at breast height (1.3 m). Tree ages are estimates based on cores collected at 1.3 m height in October 1995. For cores not including the center ring, ages are based on the estimated distance to center and mean ring widths of the five innermost rings.

Site no.	No. trees sampled	DBH (cm) Mean (Range)	Height (m) Mean (Range)	Estimated age in 1995 Mean (Range)
4	4	23 (21–28)	19 (17–25)	51 (46–6)
5	4	47 (45–49)	25 (23–26)	83 (73–98)
6	4	22 (14–40)	10 (7–14)	29 (18–44)

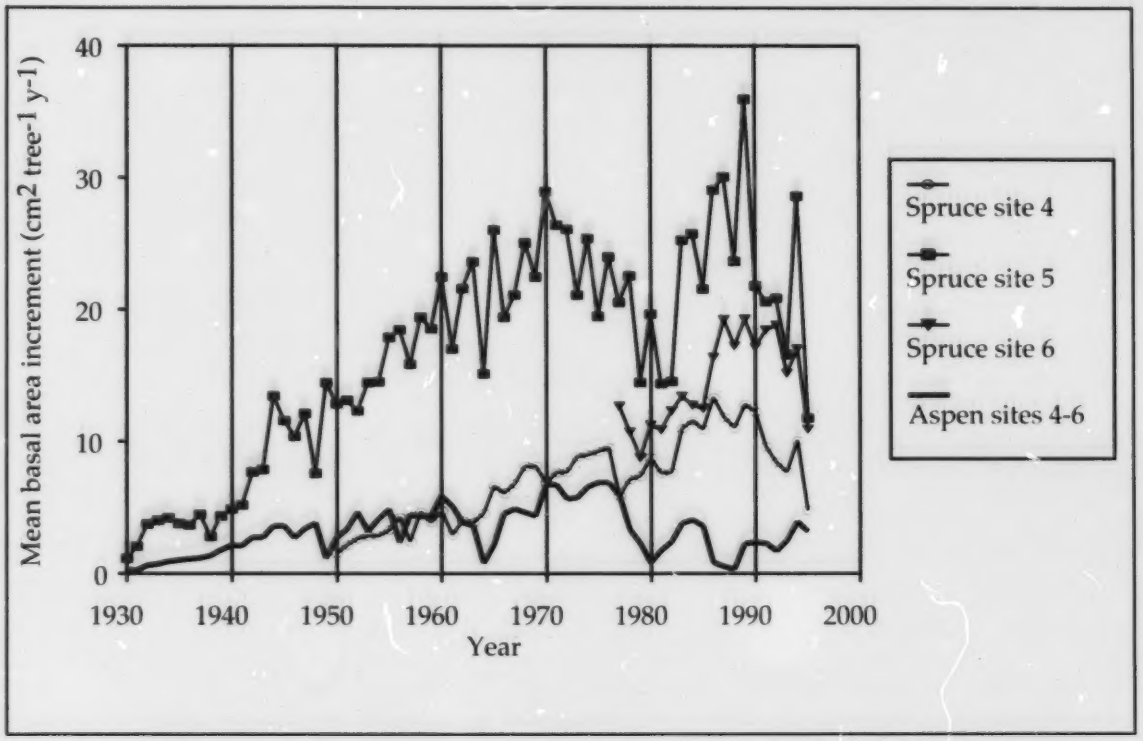

Figure 9. Average growth of 4 white spruce at each of 3 mixed-wood sites, based on dendrochronology. Also shown is average growth of 38 aspen in the same sites.

YEAR:
The number of years since 1950 (i.e., for 1995, YEAR = 45)

FTC:
This is an index of forest tent caterpillar defoliation intensity, calculated annually based on the average proportion of aspen with white rings for pure stands as a whole (bold type, Table 7).

CMI_SEA:
This is the climatic moisture index (see Methods), calculated annually based on the period from 1 September of the previous year to 31 August of the current year.

CMI_SEA[–1]:
This is the same as CMI_SEA, but lagged by 1 year (from 1 September 2 years preceding the current year, to August 31 of the year preceding the current year).

TA_GROWTH[–1]:
This is the same as TA_GROWTH, but lagged by 1 year (i.e., the year preceding the current year).

The following steps were conducted in the analysis:

1. The relationship between aspen growth (TA_GROWTH) and the climatic moisture index (CMI_SEA, CMI_SEA[–1]) was examined. Although there was a slight positive trend between moisture and growth (r^2 = 0.109), it was not statistically significant (P = 0.07 for the CMI_SEA[–1] coefficient).

2. The relationship between TA_GROWTH and the tent caterpillar defoliation index [FTC] was examined (excluding climatic factors). A moderate relationship (r^2 = 0.417) with TA_GROWTH was obtained, and the regression coefficient for FTC was highly significant (P<0.00001):

   TA_GROWTH = 4.10 – 0.0178 YEAR – 0.0372 FTC

3. The combined effects of tent caterpillar defoliation (FTC) and the climatic moisture index (CMI) were examined. This resulted in a significant improvement in the relationship (r^2 = 0.561), with highly significant regression coefficients for both FTC (P<0.00001) and CMI_SEA[–1] (P<0.001):

   TA_GROWTH = 4.88 – 0.0226 YEAR – 0.0407 FTC + 0.0262 CMI_SEA + 0.0579 CMI_SEA[–1]

   Note that the CMI for the previous year (CMI_SEA[–1]) had a greater effect than that for the current year (CMI_SEA).

4. The above analysis was repeated, but the influence of the previous year's growth (TA_GROWTH[–1]) was also included. This resulted in a much stronger relationship (r^2 = 0.832):

   TA_GROWTH = 2.33 – 0.0083 YEAR – 0.0287 FTC + 0.0191 CMI_SEA + 0.0350 CMI_SEA[–1] + 0.565 TA_GROWTH[–1]

Again, significant regression coefficients were obtained for FTC (P<0.00001) and CMI_SEA[–1] (P<0.002), while CMI_SEA was nearly significant at the 5% level (P = 0.07). This regression equation is plotted, along with the observed aspen growth, in Figure 10.

This regression equation can also be used as a preliminary means of examining the relative impacts of climate (drought) and defoliation on aspen growth. If tent caterpillar defoliation is removed by setting FTC to zero for all years, then significant improvements in simulated aspen growth are observed, particularly in the mid-1960s and 1980s (Fig. 10). Indeed, the results suggest that if defoliation had not occurred, aspen growth would have been particularly good in the late 1980s.

A crude method of examining drought impacts is to eliminate drought by setting the climate moisture index to +5 in the regression equation for all years (typical of a moist year in the Bronson Forest, see Fig. 3). With both drought and defoliation effects removed, aspen growth is simplistically represented as a slight linear decrease over time (Fig. 10). In a comparison of the two scenarios with no forest tent caterpillar, the model predictions of aspen growth under the climatic conditions experienced in the Bronson Forest are significantly reduced by drought, especially in the 1950s, the early 1980s, and the early 1990s.

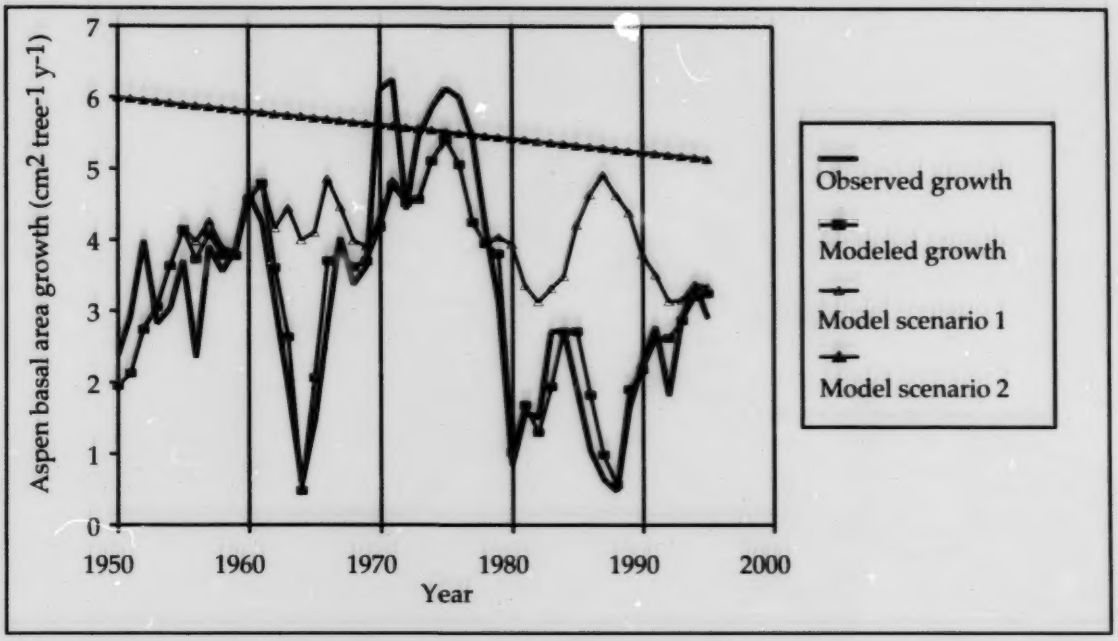

Figure 10. Statistical model of aspen growth per tree in pure stands (sites 1–3). Observed growth is based on dendrochronology. Modeled growth under the following scenarios is also shown: scenario 1, no defoliation by forest tent caterpillar; and scenario 2, no defoliation and no drought (climate moisture index set to +5 for all years).

Two other indexes of climate were also examined, including the number of growing degree days, and a summer frost index (as described in the Methods section), but neither of these were significantly related to aspen growth.

The potential impact of late winter thaw events followed by severe frost in early spring (prior to leafout) was not examined in the statistical model, because a suitable index has not yet been developed. However, an examination of the daily climate record indicated that such an event occurred in 1992. Following a period of unusually mild temperatures and scant snowfall from late February to early April (maximum temperature of 21°C on 2 April), the temperature dropped to –19°C on 10–11 April. This combination of events can cause xylem cavitation and damage to roots and buds (Cayford et al. 1959; Auclair et al. 1990, 1992; Cox and Malcolm 1997). This could have contributed to the observed aspen dieback, and may also account for the reduced growth of aspen in 1992, relative to that predicted by the statistical model (Fig. 10).

Statistical Modeling of White Spruce Responses to Climate

A similar dynamic regression approach was used to examine relationships between white spruce growth and climate, for the same period used for aspen (1950–1995). The dependent variable (WS_GROWTH) was calculated as the average of basal area increment (square centimetres per tree) for the eight spruce sampled in sites 4 and 5 (Table 8). The spruce in site 6 were excluded because of their young age.

The following equation was obtained, using the climate moisture index for 1 September of the previous year to 31 August of the current year (CMI_SEA):

$$WS_GROWTH = 11.00 + 0.1697\ YEAR + 0.132\ CMI_SEA,\ r^2 = 0.457$$

The regression coefficient for CMI_SEA was highly significant ($P<0.004$), but unlike the

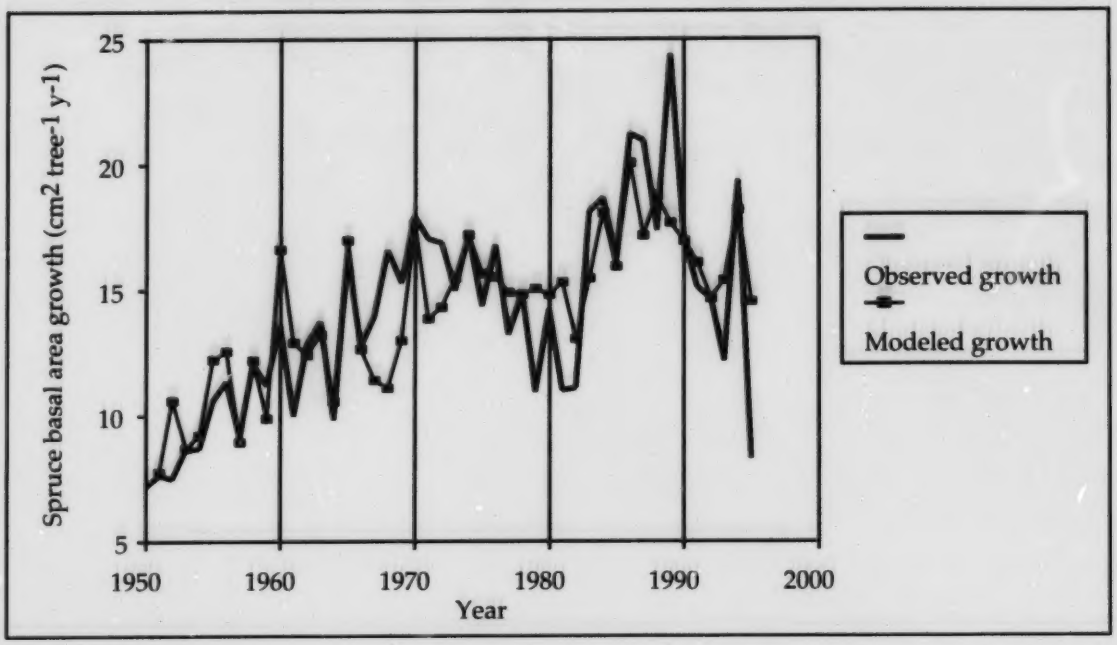

Figure 11. Statistical model of white spruce growth, based on dendrochronology.

relationship for aspen growth, the previous year's moisture index (CMI_SEA[–1]) and growth (WS_GROWTH[–1]) were not significantly related to current year growth in white spruce.

An improved relationship was obtained by using the climate moisture index based on the period 1 August of the previous year to 31 July of the current year (CMI_AUJ):

$WS_GROWTH = 11.32 + 0.1695\ YEAR + 0.161\ CMI_AUJ,\ r^2 = 0.552$

The regression coefficient for CMI_AUJ was highly significant (P<0.0002). A further improvement to the equation was obtained by also considering the number of spring growing degree days for the period ending 31 July each year (variable GDDXJUL):

$WS_GROWTH = -0.40 + 0.1453\ YEAR + 0.168\ CMI_AUJ + 0.0152\ GDDXJUL,\ r^2 = 0.602$

This equation, giving modeled white spruce growth, is shown in Figure 11, along with the observed growth of the 8 trees sampled.

It is interesting to note that the general growth pattern of white spruce appeared to be almost independent of the growth pattern of aspen (r^2 = 0.04, Fig. 9). This is partly because of the dominant role of defoliation events in governing the growth of aspen, but not spruce. Although growth patterns of both species can be partly explained by variation in the climatic moisture index, the analysis suggests that moisture in August affects radial growth of the current year in aspen but not white spruce. This could indicate that radial growth is usually completed by late July in white spruce (Sutton 1969) but not in aspen.

DISCUSSION

To our knowledge, this is the first major study in which tree-ring analysis has been used to examine growth responses of trembling aspen to the combined effects of climate and insect defoliation. We are also not aware of any previous published reference to the presence of white (light-colored) tree rings in aspen. The results of this study indicate that these white rings can be a useful indicator of past defoliation events at the individual tree and stand level. However, more detailed studies are needed to determine the chemical and anatomical characteristics of white rings, and to further clarify the precise causes of white ring development in aspen.

This study supports previous observations, which show that outbreaks of forest tent caterpillar can lead to dramatic reductions in the radial stem growth of aspen, especially following several consecutive years of severe defoliation (Duncan and Hodson 1958; Churchill et al. 1964; Hildahl and Campbell 1975). Regression modeling indicated that defoliation was the most important factor causing reduced stem growth. However, we also found that annual stem growth was significantly related to changes in moisture, as reflected by values of the climate moisture index.

The degree of crown dieback in the three decline classes in the Bronson Forest was strongly related to the magnitude of stem growth reduction following past defoliation events. Relative to the healthy stands, the growth of the heavily declining stands (>40% crown dieback) has been chronically reduced since they were defoliated in the 1960s, and their growth has been further reduced since the repeated defoliation in the 1980s. Thus we conclude that repeated defoliation, coupled with relatively dry conditions in the early 1990s, were the most important factors causing the recent crown dieback of aspen in the Bronson Forest.

Based on these results, the long-term future productivity and health of existing aspen stands in the Bronson Forest and elsewhere in the region will likely depend strongly on the future dynamics of forest tent caterpillar. There is also a wide variety of other insects and fungal pathogens that cause reduced growth and increased mortality of aspen (see Hiratsuka 1987; Ives and Wong 1988; Hiratsuka et al. 1990; Moody and Amirault 1992; Brandt 1995). For example, trees repeatedly defoliated by forest tent caterpillar may be vulnerable to infestations of the bronze poplar borer (Ives and Wong 1988), which can then provide a pathway for secondary fungal infections. Another major defoliator of aspen is the large aspen tortrix, which causes reduced growth.

It is also important to consider the potential impacts of extreme weather events, and how the frequency of these events might be affected under climate change. Drought might be the most significant concern in this respect, and an example of its effects is shown by the losses of riparian poplar forests following lowered water tables after damming of rivers in southern Alberta (Rood and Heinze-Milne 1989). Other types of extreme weather events that could cause damage to forests include hail (Riley 1953) and thaw–freeze events during late winter and early spring (Cox and Malcolm 1997; Auclair et al. 1990, 1992; Cayford et al. 1959). Such an event occurred in the Bronson Forest in 1992, when unusually mild conditions in late winter were followed by a severe frost in April. This event may have been a contributing factor to the aspen dieback observed in the present study, but further research is needed to determine its relative importance in causing aspen decline at the regional scale.

Based on the analyses of this study, the severity of drought presently encountered in the western Canadian boreal forest is not likely to cause a major decline of aspen, unless it occurs in combination with other stresses. Climate change, however, could lead to more severe drought in this region in the future, similar to that typically encountered of the aspen parkland (Hogg and Hurdle 1995). If this occurs, then more severe dieback of aspen may be expected following defoliation events (Hogg 1999). An additional concern is that the frequency of outbreaks could increase under climate change, based on studies showing that this insect is inhibited by cold springs (Blais et al. 1955) but thrives under warm, dry summers and mild winters (Ives 1981).

The climate record indicates that significant warming has already occurred, but there is not

yet any clear evidence of a trend toward drier climatic conditions. An alarming recent development of a major infestation of forest tent caterpillar was recorded for the first time in 1995 along the Liard River in the Northwest Territories (Brandt et al. 1996). This could indicate that recent climatic warming is leading to a northward range extension of the outbreaks of this species.

In this study, tree-ring analysis of a limited sample of white spruce in the Bronson Forest indicated excellent growth of this species since the early 1980s, during the same period when the aspen was showing very poor growth. It may thus be useful to examine the potential silvicultural options for establishing white spruce in situations where pure aspen stands are in heavy decline, e.g., by seeding or underplanting of seedlings.

In conclusion, it is clear that the effects of both defoliation and climatic events need to be considered when predicting future growth and yield of aspen. The results of this study also showed that dieback of aspen in the Bronson Forest was preceded by a period of reduced radial growth. Thus, advance warning of future dieback events in the region could be provided through annual assessments of forest health, coupled with periodic assessments of radial growth through tree-ring analysis.

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